

CHAPTER 12

LONG-TERM POPULATION FLUCTUATIONS OF A TROPICAL LIZARD: A TEST OF CAUSALITY

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A central problem in ecology concerns population stability. Connell and Sousa (1983) point out that the assumption of constancy through time is implicit to a wide range of theoretical and empirical studies on ecological systems. Given this assumption, observations of resource partitioning, for example, can be used imply to past and present competition for resources. If, on the other hand, populations fluctuate widely, present patterns of resource use may have little relationship to past interactions among species (Wiens 1977). Actually, in a survey of real populations, magnitude of population fluctuation varied widely (Connell and Sousa 1983). No taxonomic patterns were apparent in this survey; terrestrial plants, terrestrial insects, aquatic invertebrates, birds, and mammals all included populations with low and with high variability in density. Lizards, however, were not included in Connell and Sousa's study.

In fact, observations of 29 populations of 21 species over relatively short periods suggest that constancy through time is characteristic of lizard populations (Schoener 1985). This idea is supported by long-term observations published more recently (Abts 1987; Jones and Ballinger 1987; Strijbosch and Creemers 1988; McLaughlin and Roughgarden 1989). However, concluding that lizard populations are unusually stable from this data set may be premature. One limitation of the data concerns geography; most observations were either for species inhabiting temperate zone regions or small islands in the West Indies. These locations are unlikely to be representative of all habitats occupied by lizards. Another limitation concerns life histories; most observations were for species in which adults are relatively long lived. In this situation, a persistent adult population buffers the effect of variable reproductive success. For example, chuckwallas (*Sauromalus obesus*) in the southwestern U.S. breed infrequently; reproduction is associated with years of high rainfall when food is abundant (Abts 1987). Still, the population fluctuates little because of high adult survival from one year to the next.

We use long-term data on populations of the polychrid (sensu Frost and Etheridge 1989; formerly in the Iguanidae) lizard *Anolis* limifrons* to address the issue of stability. The geographic range of *A. limifrons* is mainland neotropical, and individuals are relatively short lived. Thus, this species provides a geographical and life-history contrast to the majority of

population studies on lizards. In addition, we will go beyond a description of population fluctuations and discuss the results of an experimental study that tests causal mechanisms behind changes in population density.

In comparison with other lizard species, populations of *A. limifrons* are far from stable. This conclusion is the result of observations for 22 years at Barro Colorado Island (BCI) in Panama (Fig. 12.1). During this period, the population has exhibited large fluctuations in density from one year to the next and even larger variation over decades (Andrews 1991).

Fluctuations in density are correlated with variation in the amount and timing of rainfall (Andrews and Rand 1982, 1990; Andrews 1991). Thus, rainfall appears to drive the large fluctuations in density, although food intake and recruitment are density dependent. *Anolis limifrons* individuals are most abundant at the end of years with wet seasons that are relatively dry, and with dry seasons that are relatively short, as measured by the amount of rainfall during the preceding December and April. December and April are critical months in defining the length of the dry season. For example, if much rain falls in December and April, the dry season is short (3 mo), and if little rain falls in December and April, the dry season is long (5 mo). In contrast, the months of January through March are not relevant (statistically) because rainfall is consistently low.

The two components of the correlation between population density and rainfall are the amount of rain in the wet season and the length of the dry season. Of these two, the association between the length of the dry season and population density makes the most sense. The dry season is a period of very low reproductive activity (Andrews 1979a). For example, at the beginning and end of the dry season, December and April, the number of eggs in the forest is 24% and 4%, respectively, of that during the middle of the wet season (July-September) when egg production is maximal (Andrews unpubl.). Low reproduction in the dry season can be related to population density at the end of the year because recruitment commences when the rains begin in April or May, and the sooner the rains begin, the longer the period in which individuals are added to the population and the larger the population build-up by the end of the year.

The second component of the correlation between rainfall and population density is the amount of rain during the wet season. At the time the experimental component of this study was initiated, we did not know why a wet season with low rainfall was associated with high population density. As we shall discuss, the consequences of manipulations of moisture availability in the dry season suggest a mechanism that relates the amount of rainfall during the wet season to population density.

* Editors' note: Nomenclature of anolines remains controversial; *Anolis* was split by Guyer and Savage (1986), reconsidered by Cannatella and de Queiroz (1989) and Williams (1989), and further reconsidered by Guyer and Savage (1992).

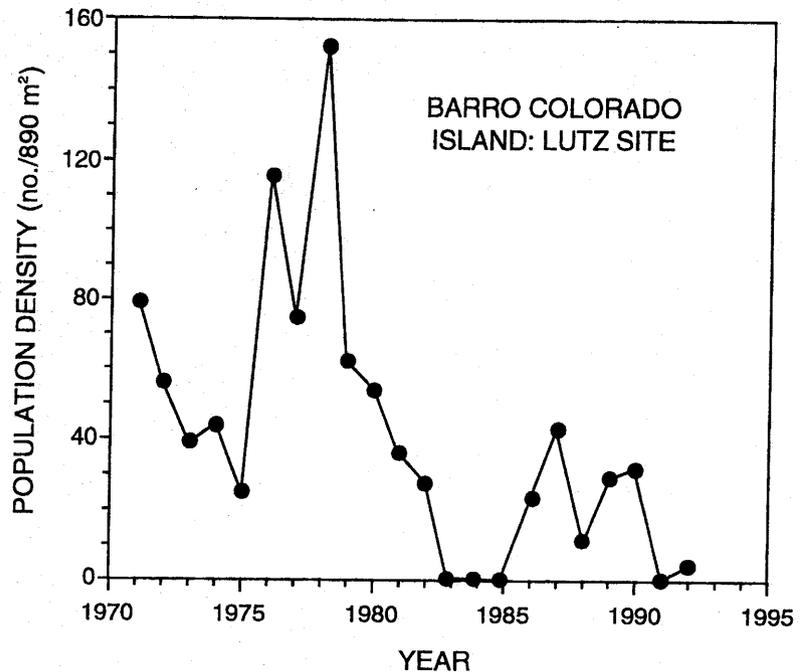


Figure 12.1. Population density of *A. limifrons* at Lutz site at Barro Colorado Island, Panama from 1971 through 1992. Data for 1971–1989 are from Andrews (1991) and data for 1990–1992 are from Andrews and Rand (unpubl.).

The opportunity to evaluate the mechanism or mechanisms by which seasonal variation in rainfall affects population density was provided by a major experimental perturbation at BCI. Water was provided to large areas of rainforest during three successive dry seasons. The amount of water was sufficient to maintain soil moisture and relative humidity near the forest floor at wet-season levels (Wright and Cornejo 1990). Because lizards typically perch less than 1.5 m from the ground, and eggs are laid on or near the ground, dry season conditions were ameliorated by the watering treatments for both lizards and eggs.

Our general expectation was that the density of lizards on watered plots would increase relative to that on control plots over the course of the experiment. Our reasoning was that females would produce eggs during the dry season on watered plots. Reproduction during the dry season, in addition to the wet season, would increase population density because females would produce more eggs during their lifetimes. Furthermore, whereas one generation per year is typical for this species, two generations per year would be possible if reproduction were possible year round.

Materials and Methods

Life history

The life history of *A. limifrons* in Panama is well known (Sexton 1967; Sexton et al. 1972; Andrews 1979a, 1982b; Andrews and Rand 1982, 1983; Andrews et al. 1983; Wright et al. 1984). Pertinent attributes are summarized here. *Anolis limifrons* is a small lizard with a maximum snout-vent length (SVL) and mass (M) of 50 mm and 2 g for both females and males. Females and males become sexually mature at a minimum of 35–36 mm SVL; we considered individuals of 36 mm or more to be adults. The modal size of sexual maturity for females is 41–42 mm SVL and all females are sexually mature at 44 mm SVL.

Reproduction is seasonal, with the highest rates of egg production in the early and middle wet season and the lowest rates during the dry season. Eggs are first laid when rains begin in April or May. Hatching occurs 6 weeks after oviposition and hatchlings are most abundant in August and September.

The reduction of egg production in the dry season seems more related to the effect of dryness per se on eggs than to limited food availability for lizards. Eggs laid in the dry season are subject to desiccation, at least in some years (Andrews and Sexton 1981). In contrast, lizards appear to accommodate to relatively dry conditions (Sexton and Heatwole 1968) by utilizing relatively mesic microhabitats during the dry season; lizards perch closer to the ground and are associated with larger trees during the dry than the wet season (Andrews unpubl.). Despite the fact that arthropod abundance reaches annual lows late in the wet season and during the dry season (Smythe 1982; Levings and Windsor 1982), food availability during the dry season cannot be severely limiting as juveniles grow to maturity during this period (Andrews et al. 1983), and adults increase their fat reserves (Sexton et al. 1971).

Study site and experimental procedures

Studies were conducted at Poacher's Peninsula on Barro Colorado Island (Wright and Cornejo 1990). The forest is among the oldest on BCI and has not been cleared for at least 500 years (Piperno 1990). The terrain is flat or gently sloping and the canopy is approximately 30 m high. Four 150 × 150 m plots were established in late 1984. Water availability was manipulated by watering two of the plots (plot numbers 1 and 2). The remaining plots (plot numbers 3 and 4) served as nonwatered controls. Water was delivered by PVC pipe to 80 sprinklers per plot, mounted 1.8 m above the ground. The objective was to maintain soil water potentials at -0.04 MPa at depths of 25 and 45 cm (Wright and Cornejo 1990). Thus, the schedule for watering was

adjusted relative to target levels; watering was initiated in December and continued into April for the three years of observation reported here (1986, 1987, and 1988). During a typical week in the dry season, each manipulated plot received 675,000 kilograms of water during 1.5 h between 1100 and 1400 h on each of five days. Water was taken from Gatun Lake where nutrient concentrations are lower than in rainwater (Gonzalez et al. 1975).

Demographic studies

Lizards were censused on two 30 × 30 m areas (replicates) within each of the four plots. These permanent subplots were picked randomly. Censuses were of two types. During the first type, an observer walked a set path on the perimeter and the two midlines of each 30 × 30 m area and searched for lizards 2 m either side of the transect line. During the second type of census, the 30 × 30 m areas were carefully searched for lizards. Censusing began in January 1986 and ended in October 1988. Twenty-three censuses were conducted: 4, 5, 3, 5, 3, 3 in the 1986 dry and wet seasons, the 1987 dry and wet seasons, and the 1988 dry and wet seasons, respectively. Plots were censused within a few days of one another and comparable effort was spent on all plots within each census period. Lizards captured during both types of censuses were processed and released at the site of capture. Lizards were weighed to the nearest 0.1 g using Pesola® scales and measured from the tip of the snout to the vent (SVL) to the nearest mm. Lizards were individually marked by clipping the terminal phalange of toes (not more than two toes per foot and five toes per individual). Capture-recapture data were used to estimate population density, survival, seasonality of recruitment, an index of condition, and body growth.

Data analyses

Overall, the objective of the experiment was to determine the effects of watering during the dry season on lizard populations. Because observations were made for three years, differences among years were also of interest as a main effect and as an interaction with time of year (January-April: dry season, and May-December: wet season) and treatment (watered or control). Pairwise *z*-tests follow White et al. (1982). All other statistical analyses were conducted using SAS statistical software (SAS 1982).

Standard Jolly-Seber models (Pollock et al. 1990) were used to estimate population density and survival. Data for the two subplots within each plot were pooled to ensure that sample sizes were sufficiently large for reliable estimates. Separate analyses were run using the entire data set and for adult data only. Censusing protocols differed somewhat from census to census. The first three and last three censuses were line-transect censuses while during the middle of the study, line-transect censuses were alternated with

more intensive searches of entire subplots. The lower intensity of censusing early and late in the study should tend to inflate estimates of density and reduce estimates of survival at these times. However, as the same protocols were used at all sites within any one census, estimates of numbers and survival are consistent relative to one another across sites. For statistical comparisons, we used the means of estimates of numbers and survival for each season and year combination per plot as observations in an ANOVA with repeated measures on season and year.

The proportion of individuals less than 30 mm SVL (< 2 mo old) captured during each season in each year was used as an index of recruitment. Recruitment in this sense has two components: the rate at which eggs are produced and their rate of survival to hatching. In a previous study, Andrews (1988) determined that the proportion of young individuals in *A. limifrons* populations at the end of the wet season was directly related to the survival of eggs during that wet season. For statistical comparisons, we used the proportion of individuals less than 30 mm SVL in each of the four subplots per treatment (watered vs. control plots) as observations in an ANOVA with repeated measures on season and year. Proportions were based on the first capture of an individual in each season and year, that is, each individual was represented only once per season and year combination.

An index of condition [$IC = (Mass^{0.3}/SVL) * 100$] was used as a general measure of food intake by adult males and females and of reproduction by adult females (Andrews 1991). Observations for females and males were analyzed separately because of known sexual differences in this index: IC for adult females is relatively high because of the mass of follicles and oviductal eggs (Andrews et al. 1983). Repeated observations on the same individuals in successive censuses were treated as independent observations because (1) size and reproductive status of individuals change with time and (2) recaptures were not common; the probability that a lizard alive at any one census would be captured during that census was relatively low (24–27%, results of Jolly-Seber analyses). The four subplot means per treatment for each season in each year were used as observations in an ANOVA with repeated measures on season and year.

Growth data were fitted to the logistic growth equation because it provided the best description of growth for *A. limifrons* in previous analyses (Andrews et al. 1983). The linear form of this equation is

$$SVL2 = SVL1 * a/[SVL1 + (a - SVL1) * e^{-rD}]$$

where SVL1 and SVL2 are the snout-vent lengths at the first and second capture, respectively, D is the interval in days between captures, a is the asymptotic SVL, and r is the rate constant of the logistic equation (Schoener

and Schoener 1978). Intervals < 15 d were not used. Estimates of a and r were determined by nonlinear regression procedures. To avoid bias, records for individuals that had reached their asymptotic size (SVL > 43 mm) at first capture were not used. Preliminary analyses showed that males and females did not differ in their asymptotic size or in their rate constants ($P > 0.5$, t -tests; see also Andrews et al. 1983). Therefore, data for males and females were combined.

To estimate a and r accurately, nonlinear regression analysis requires a relatively large number of records that span the range of possible sizes (see comments by Andrews in Schoener and Schoener 1978). Too few growth records were available for simultaneous comparisons of plots within treatments, years, and seasons. For example, most (70%) dry season records were from 1987, while 95% of wet season records were from 1986 and 1987. Therefore, a single estimate of a and r were made for the watered and control plots by season.

As maximum SVL for *A. limifrons* individuals is 50 mm, many individuals with SVLs of 44 mm or more were still increasing in size. To further evaluate possible differences between the treatments, growth rates (mm/d) for individuals with SVL > 43 mm were used in a three-way ANOVA with treatment, year, and season as main effects.

Egg survival was evaluated in July and August 1986 on the four plots. Details of this study were presented by Andrews (1988).

Results

Population density

Watering was initiated at the beginning of the 1986 dry season. At this time, mean estimated population density (standard errors) of adults was of 117 (53), 64 (52), 114 (161), and 29 (14) for plots 1–4, respectively. Densities on the four plots were similar (all $P_s > 0.05$, pairwise z -tests).

Adult densities during the 1986 dry season represent pretreatment densities because the great majority of these individuals would have been present when watering began. Thus, differences in recruitment or subsequent differences in density between treatments should reflect treatment effects and not preexisting differences in density.

Watered and control plots had very different patterns of population density over the course of the study (Fig. 12.2). Population densities on control plots were stable. In contrast, while densities were similar initially on watered and control plots, during the 1986 wet season, densities on watered plots exploded. At that time, all four possible pairwise comparisons between watered and control plots were statistically significant ($z_s = 1.96, 2.19, 2.82, 2.85, P_s < 0.05$). Following 1986, densities on watered plots declined

monotonically, and were again similar to control plots toward the end of the study. No pairwise comparisons at periods other than the 1986 wet season were statistically significant ($P > 0.05$). Overall, total population densities on watered plots were significantly higher than on control plots (Table 12.1). Density did not differ as a function of season, although the significant season * year interaction presumably reflects the increase in density from the dry to wet season in 1986 and the decrease from dry to wet season in 1987 and 1988. Density did not differ as a function of year, but near significance ($P < 0.10$) of this main effect and of the year * treatment interaction reflect the very different patterns of density change on the watered and control plots.

Any sampling biases (see "Materials and Methods: Data Analyses") would not have affected results of comparisons between treatments. Bias would have affected all plots, and would have resulted in relatively high estimated densities for the 1986 dry season and the 1988 wet season.

Survival

Survival of adults was not affected by watering and did not differ among years or between seasons (Table 12.1, Fig. 12.3). As predicted by the low sampling effort for the 1986 dry season and the 1988 wet season (see "Materials and Methods: Data Analyses"), estimates for these periods were relatively low. However, results of an ANOVA which excluded these two periods were the same as those utilizing all periods (Table 12.1); the only significant term in both analyses was the season * year interaction ($P < 0.05$).

In general, survival rates of adult *A. limifrons* on the watered and control plots were similar to those observed at other sites in central Panama (Wright et al. 1984; Andrews and Nichols 1990). Andrews and Nichols (1990) did not detect differences in survival rates between adults and juveniles at two other BCI sites. Similarly, overall estimates of survival in this study for analyses that included all individuals and that included only adults were virtually identical for all plots.

Growth

Watering during the dry season affected growth rates but not asymptotic size (Table 12.2). The rate constant of the logistic growth equation in the dry season on the watered plots (0.023) was higher than on the control plots (0.019). Given the a priori assumption that lizards should grow faster under moister conditions (Stamps and Tanaka 1981), this difference was statistically significant ($P < 0.05$, $t = 1.8$, one-tailed t -test). Lizards had similar growth rates on the watered and control plots in the wet season, and asymptotic sizes were similar at all times ($P > 0.05$, t -tests). At these growth rates, a hatchling would grow to sexual maturity (36 mm SVL) in 68 days in the dry season on the watered plots, but this growth would take 81–83 days in the

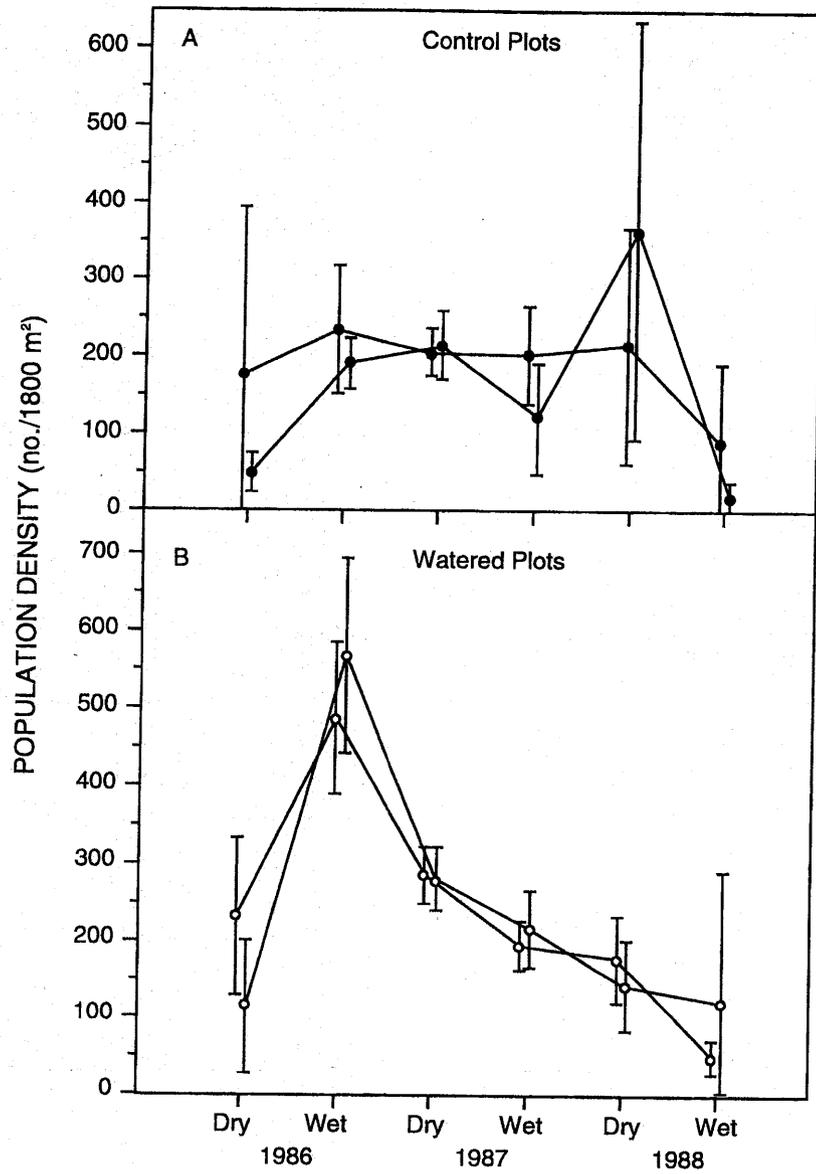


Figure 12.2. Estimates of population density ($\pm 1 SE$) of *A. limifrons* on control plots (top panel; closed circles) and watered plots (bottom panel; open circles). Estimates are arithmetic means of time-specific estimates for each season and year combination. Standard errors are pooled standard errors for these periods.

Table 12.1. Repeated measures analyses of variance for population density and adult survival. Where appropriate, Greenhouse-Geisser estimates of probability levels are given. Means are shown in Figs. 12.2 and 12.3, respectively.

Source	df	Density		Survival	
		F	P	F	P
Between subjects					
Treatment	1	21.2	< 0.05	1.0	0.41
Error	2				
Within subjects					
Season	1	0.0	0.92	0.0	0.88
Season*Treatment	1	3.6	0.20	0.3	0.66
Error	2				
Year	2	11.2	< 0.10	0.2	0.74
Year*Treatment	2	12.6	< 0.10	0.1	0.76
Error	4				
Season*Year	2	21.2	< 0.05	26.5	< 0.01
Season*Year*Treatment	2	2.7	0.18	1.3	0.37
Error	4				

wet season on all plots and in the dry season on the control plots. In contrast, growth rates of adults with SVLs > 43 mm did not differ as a function of treatment, season, or year ($P > 0.05$, $F_{11,386} = 1.2$, 3-way ANOVA).

Index of condition

Results of the analyses of IC were similar for females and males (Table 12.3). As expected, however, absolute values of IC were higher for females than males (Fig. 12.4). IC did not differ between watered and control plots. Except for the dry season of 1988, values of IC were highest during the dry season and lowest during the wet season, and these seasonal differences were significant. IC declined during the 1986–1988 period, and differences among years were significant as well. The season by year interaction was significant, presumably because of the relatively low values for IC in the 1988 dry seasons.

Juvenile recruitment

The proportion of juveniles did not differ between treatments (Table 12.4, Fig. 12.5). However, seasonal variation was highly significant as was the season * treatment interaction. This interaction reflects the very different pattern of recruitment on watered and control plots. Recruitment on control

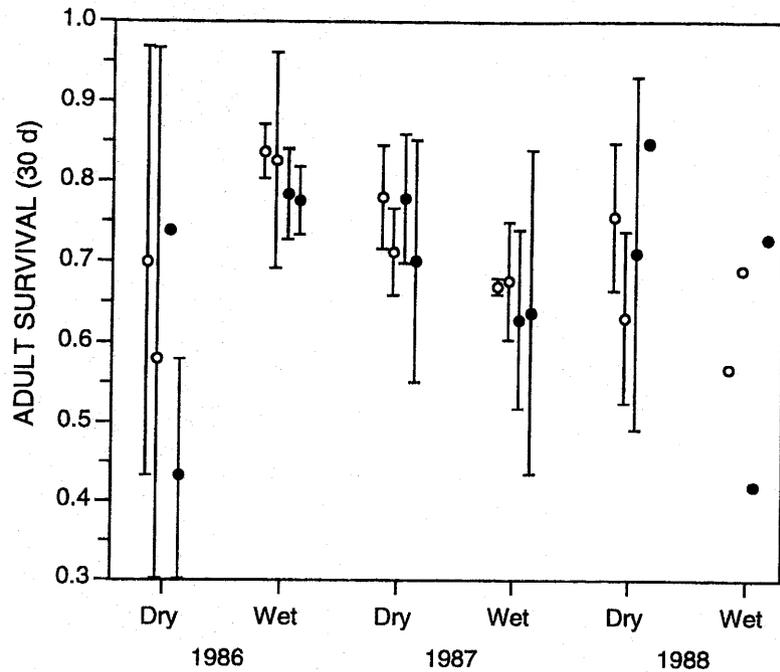


Figure 12.3. Estimates of 30-day probabilities of survival ($\pm 1 SE$) for adult *A. limifrons* on two control (closed circles) and two watered (open circles) plots. Estimates are arithmetic means of time-specific estimates for each season and year combination. Standard errors are pooled standard errors for these periods (Nichols pers. comm.). Standard errors could not be calculated for some estimates early and late in the study period.

plots was strongly seasonal—relatively few juveniles were present during the dry season and relatively many were present in the wet season. In contrast, on watered plots the proportion of juveniles did not change seasonally. This pattern was consistent across years.

Egg survival

Egg survival from oviposition to hatching was higher on the two watered plots (25% and 42%) than on the control plots (15% and 8%) ($P < 0.01$, $2 \times 2 X^2$ test) in July and August 1986 (Andrews 1988).

Discussion

Population dynamics

Barro Colorado Island supports a semideciduous tropical forest. Rainfall is seasonal, but only a small minority of tree species are deciduous during the

Table 12.2. Fitted parameters of the logistic growth equation for *A. limifrons* populations in dry and wet seasons on watered and control plots. Estimates of a (asymptote) and r (rate coefficient) are followed by n , asymptotic SE (in parentheses). N. S. = not significant.

	Season	
	Dry	Wet
Asymptote, a		
Watered	47.1 (63, 0.56)	47.3 (76, 0.44)
	N. S.	N. S.
Control	47.5 (59, 0.62)	47.0 (64, 0.59)
Growth Constant, r		
Watered	0.023 (63, 0.0018)	0.019 (76, 0.0011)
	$P < 0.05$	N. S.
Control	0.019 (59, 0.0015)	0.019 (64, 0.0013)

Table 12.3. Repeated measures analyses of variance for the index of condition for females and males (mean values shown in Fig. 12.4). Where appropriate, Greenhouse-Geisser estimates of probability levels are given.

Source	df	Females		Males	
		F	P	F	P
Between subjects					
Treatment	1	0.2	0.67	1.0	0.36
Error	6				
Within subjects					
Season	1	26.5	< 0.01	57.6	< 0.01
Season*Treatment	1	3.0	0.13	1.1	0.34
Error	6				
Year	2	5.9	< 0.05	24.3	< 0.01
Year*Treatment	2	0.8	0.48	0.4	0.67
Error	12				
Season*Year	2	12.7	< 0.01	12.2	< 0.01
Season*Year*Treatment	2	0.4	0.62	1.8	0.22
Error	12				

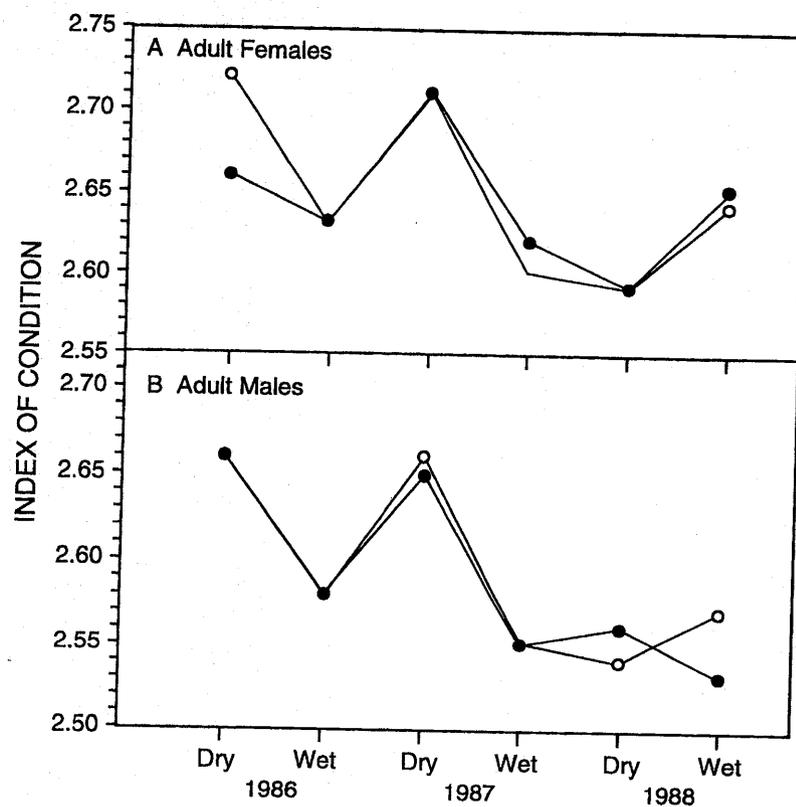


Figure 12.4. Index of Condition (IC) for adult females and males on control (closed circles) and watered (open circles) plots. Because of extensive overlap, SEs are not shown.

dry season (Foster and Brokaw 1982). Still, variation in rainfall affects phenology and reproductive success of both plants and animals (Leigh et al. 1982). Some species of plants and animals found in wetter habitats only a few kilometers to the east are not present on BCI, and others more typical of wetter habitats are also found on BCI. For example, *A. limifrons* and its congener *Anolis humilis* are sympatric in the aseasonal rainforests of the Atlantic lowlands of Panama and the rest of Central America. *Anolis humilis* does not occur on BCI or in other places with pronounced seasonality. On the other hand, the range of *A. limifrons* does extend into relatively seasonal habitats, but its distribution as a whole is largely coincident with that of aseasonal rainforests. What features of the dry season at BCI are inimical to *A. limifrons*—a species more typically associated with less seasonal habitats? Our experimental manipulations address this question. Watering during the dry season resulted in a population outbreak of *A. limifrons* during the 1986

Table 12.4. Repeated measures analysis of variance for the proportion of juveniles < 39 mm SVL captured during each season in each year (values shown in Fig. 12.5). Proportions were arcsine transformed before analysis. Where appropriate, Greenhouse-Geisser estimates of probability levels are given.

Source	<i>df</i>	<i>F</i>	<i>P</i>
Between subjects			
Treatment	1	0.3	0.61
Error	6		
Within subjects			
Season	1	85.5	<0.01
Season*Treatment	1	46.9	<0.01
Error	6		
Year	2	0.0	1.00
Year*Treatment	2	2.8	0.12
Error	12		
Season*Year	2	0.3	0.74
Season*Year*Treatment	2	1.6	0.25
Error	12		

wet season. Population densities on watered plots were 500 or more individuals per 1800 m², which was higher than has been previously recorded on BCI (Andrews et al. 1983). Densities on watered plots during the outbreak were more like those of West Indian islands than mainland sites (Andrews 1979b). In contrast, during the 1986 wet season, population densities on control plots were less than half those on watered plots.

Adult lizards were apparently unaffected by the experimental maintenance of wet-season levels of moisture during normally dry periods. Adult survival did not vary between watered and control plots. Adults on watered and control plots had virtually identical patterns of their index of condition. In general, high values of IC are associated with relatively high food intake, while for females, high values of IC are associated with enhanced rates of egg production (Andrews 1991). Thus, food availability and egg production should have been similar on the watered and control plots. Why did watering during the dry season not affect adult lizards? To address this question, *A. limifrons* populations must be placed in the context of their position in a very complex food web (Pimm 1991). The response of the forest to watering in the dry season was limited. For example, most species of trees were unaffected in terms of seasonal patterns of leaf flush, leaf drop, and fruit production (Wright and Cornejo 1990). In the understory, the phenology of some

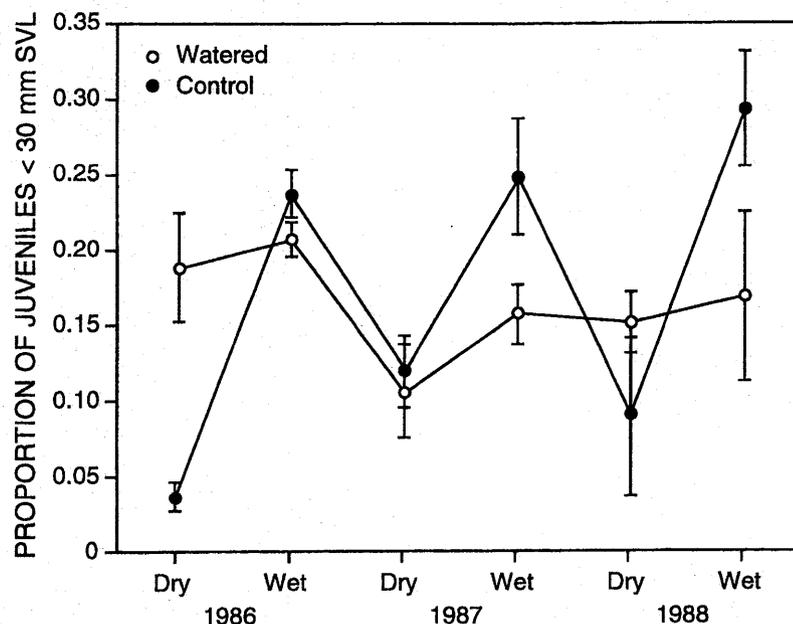


Figure 12.5. Pattern of recruitment as indicated by the proportion (± 1 SE) of individuals less than 30 mm SVL on control (closed circles) and watered (open circles) plots.

shrubs was shifted by watering, but productivity overall was not altered (Wright 1991). Thus, for the plant community, production and phenology were little affected by alleviation of water stress during the dry season. Overall, the abundance of arthropods, including prey taxa eaten by *A. limifrons*, did not differ between the watered and control treatments, although arthropod abundance was generally higher in 1986 than in 1987 or 1988 (Wolda and Wright 1992). Observations on arthropod abundance are thus compatible with the patterns of variation in the index of condition, and both indicate that prey availability to *A. limifrons* individuals was not affected by the watering treatment. Judging by the similar rates of survival for *A. limifrons* on the watered and control plots, overall predation rates were also unaffected by the watering treatment. This suggests that predator populations were unaffected by watering or that net predation on *A. limifrons* populations did not change. Literally scores of species are predators on *A. limifrons*. These include mammals, birds, snakes, and other lizards, as well as invertebrates such as spiders and mantids. Responses by such diverse taxa to watering could be quite variable without any obvious change in the mortality of one prey species. Given that the food web was not disrupted by watering during the dry season, it is perhaps not surprising that survival and food

intake for *A. limifrons* individuals were not affected by what, at first sight, was a major environmental perturbation. We assume that the lack of response to the watering treatment by adult lizards can be extended to juveniles as well. Adults and juveniles have similar rates of survival (Andrews and Nichols 1990) and eat the same types of prey (Sexton et al. 1972).

In contrast to the "lizard" stage, the egg stage was strongly affected by the watering treatment, and the population process most closely linked to the outbreak in 1986 and the subsequent population decline on the watered plots was variation in egg survival. Watering had a marked effect on recruitment (Fig. 12.5). Normally, the proportion of juveniles is low in the dry season and high in the wet season when most egg laying occurs. This was the pattern of recruitment on the control plots. In contrast, on watered plots, recruitment into the population was initiated early in 1986; young juveniles made up an unusually large proportion of the population in the 1986 dry season. Because recruitment started early, more individuals were added to the populations on watered than control plots. Enhanced survival of eggs during the 1986 wet season (Andrews 1988) also would have contributed to the increase in population density on the watered plots in 1986. Moreover, given observed growth rates, hatchlings produced in the dry season on the watered plots would have matured, and their offspring would have been in the censused population during the following wet season. However, in 1987 and 1988, the proportion of young juveniles on watered plots was the same as on control plots in the dry season and considerably lower in the wet season. As adult survival did not vary with treatment, we conclude that the population decline in 1987 and 1988 was the result of relatively low recruitment on the watered plots.

Causality?

If recruitment were enhanced by amelioration of dry season conditions on the watered plots in 1986, why was it not enhanced in the following two years? One explanation is that the response to watering in the dry season was a function of prevailing ambient conditions.

Population density is correlated with rainfall. Thus, the overall response to watering during the dry season should reflect, what, on the basis of rainfall, are good and bad years for population growth. *Anolis limifrons* individuals are more abundant at the ends of years when rainfall during the wet season is relatively low and when the dry season is relatively short. In this regard, 1986 should have been a particularly favorable year for populations of *A. limifrons*. In 1986, annual rainfall at BCI was 217 cm with December and April rainfall totalling 49 cm. In contrast, in 1987 and 1988, annual rainfall was relatively high, 295 cm and 260 cm, respectively, while December and April rainfall was low, 40 cm and 21 cm, respectively. Given the amount

and pattern of rainfall during 1986 through 1988, population densities in the 1986 wet season should have been higher than in the 1987 and 1988 wet seasons. Furthermore, in 1986, the combination of watering during the dry season plus low rainfall during the wet season should have provided ideal conditions for an increase in population density on watered plots relative to the control plots. On the other hand, in 1987 and 1988, high rainfall in the wet season was not favorable for population growth, and differences in density between watered and control plots should have been lower during these years than in 1986. This is exactly the pattern observed. Densities on watered plots were higher than those on control plots in 1986 but not in the other two years. Apparently, watering during the dry season did not compensate for the effect of high rainfall in 1987 and 1988.

Year-to-year changes in IC support the idea that environmental conditions deteriorated over the 1986-1988 period. Lizards were in better condition in 1986 than in the following years irrespective of treatment. This suggests that food intake and reproductive output would have been highest in 1986, and lower in 1987 and 1988. Moreover, as IC was similar on the watered and control plots, the decline in IC must have been associated with changes in environment that were unrelated to effects of watering.

While changes in population density and IC of *A. limifrons* on the watered and control plots were consistent with the hypothesis that responses were a function of ambient weather conditions, the pattern of recruitment was not. Watering during the dry season should have enhanced recruitment irrespective of rainfall, and recruitment during the wet season should have been similar on the watered and control plots irrespective of rainfall. This was observed in 1986, but not afterwards. Instead, in 1987 and 1988, recruitment during the dry season was similar on the watered and control plots, and recruitment during the wet season was depressed on watered plots relative to control plots.

This problem is resolved if we consider that watering the second or third years, may not have been a simple replication of the first year. Watering in successive years could have changed the environment so that some factor or factors became detrimental to either the rate of egg production or to egg survival. The similar values of IC for females indicate that the rate of production of eggs probably did not differ between watered and control treatments. If this is correct, then continued watering must have had an inimical effect on egg survival. We speculate that continued wet conditions were associated with the build-up of pathogens or predators normally reduced in numbers by dry conditions. Such an effect would be consistent with the relatively low recruitment on the watered plots in 1987 and 1988, and the (apparently) monotonic decline of population density on the watered plots. It is also consistent with known interactions between *Solenopsis* ants, the

major predator on eggs (Andrews 1988), and moisture. *Solenopsis* are more abundant in the wet than the dry season, are more abundant in wet than dry microhabitats at any time of the year, and increase in numbers when plots are watered experimentally in the dry season (Levings 1983; Kaspari pers. comm.).

Results of the watering experiment suggest causal mechanisms behind the correlation between population size and rainfall. First, because egg production by *A. limifrons* is a facultative response to moisture, short dry seasons enhance the rate of population growth by simply increasing the time during the year available for reproduction. A longer reproductive season means that more individuals can be recruited into the population. More eggs are produced by individual females over their lifetimes, and eggs produced early in the breeding season can give rise to a second generation that season. Second, because egg survival is enhanced if the wet season is relatively dry and reduced if the wet season is relatively wet, the amount of rainfall during the wet season is negatively related to population density by the end of the wet season.

The first of these mechanisms is actually a description of known features of the demography of *A. limifrons*. The second is speculative, but plausible, and would be relatively easy to test. The critical result at this point is, however, that abundance of this tropical lizard is critically related to variation in the physical environment. Variation in rainfall affects when and how long eggs are produced and, through the effect of rainfall on egg predators or pathogens, how many eggs survive.

Conclusions

Results of this study provide insights that should be helpful with regards to one of the critical issues in the coming decades of research on lizards. This issue is the recognition and conservation of endangered species or populations. The first insight is that lizard populations normally fluctuate in size, and some normal fluctuations are of high amplitude. We have documented wide temporal variation in the density of a tropical lizard. This, and observations on other species (e.g., Wolda and Foster 1978; Rand et al. 1983), indicate that species of tropical forests fluctuate just as widely as species of temperate regions. Widely fluctuating populations, irrespective of habitat, create two problems. First, distinguishing between natural declines in density and declines related to anthropogenic changes in the environment may be difficult even with studies lasting a decade or more (Pechmann et al. 1991). The second problem is that reserves set aside for conservation purposes must be sufficiently large to accommodate both the high and low points of natural fluctuations. This point is not novel, of course, as it is one of the general guidelines of conservation biology (Soulé 1987).

Another insight, which is perhaps novel, is that ecological studies that do not explicitly include the egg stage are not likely to develop a useful understanding of how both normal and anthropogenic environmental changes affect population dynamics. The reason is that lizards in eggs are more affected by variation in physical and biotic environment than lizards after hatching. Eggs are relatively small and immobile—they do not have the homeostatic abilities of lizards; eggs are stuck with their nest site while post-hatching individuals have the ability to seek out favorable microclimates and to avoid predators. Thus, similar changes in the physical and biotic environment will be harsher from the viewpoint of the egg than from the perspective of posthatching lizards. Such differences between eggs and posthatching lizards likely affect the population dynamics of all oviparous species. Thus, a thorough understanding of the dynamics of the egg stage is critical to an assessment of changes in lizard abundance (this study; Overall this volume) and perhaps also the presence or absence of a species in an area (Muth 1980). This is not to say that the relationship between variation in the physical environment and variation in population density will always be as tightly linked as we have demonstrated for *A. limifrons*. With annual population turnover and the potential for two generations per breeding season, the number of lizards at the end of the breeding season largely reflects the success of recruitment during that breeding season. This particular life cycle may lead to instability, as r , the intrinsic rate of increase, is directly related to the amplitude of population fluctuations (May 1981).

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